THE LIFE HISTORY AND BIOLOGY OF THE GENUS FRENESIA (TRICHOPTERA: LIMNEPHILIDAE).1

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The order Trichoptera, or the caddis flies, is one of the commonest orders of insects met with in any limnological survey. Yet no one has attempted to treat any species or genus morphologically and biologically throughout all its stages. The genus *Frenesia* Betten and Mosely was chosen for this study as its life cycle was, in certain respects very different from that of most caddis flies and presents several interesting adaptations. The genus contains two species, *difficilis* (Wlk.) and *missa* (Milne), which are often found flying together in the fall and early winter months in the north eastern United States.

The study was done at the state fish hatchery in Sunderland, Massachusetts, from the fall of 1953 to the spring of 1955. The fish hatchery is situated at the base of a gravel delta, deposited shortly after the last Pleistocene glaciation. A stream, which flows out onto the delta, sinks into the gravel about a mile east of the hatchery. The waters reappear at the hatchery as many springs along the margin of the delta. The water where it leaves the ground is very pure and of uniform flow and temperature (46–47° F.) throughout the year.

LIFE HISTORY

Taxonomy. Francis Walker described difficilis in 1852 from a specimen taken in Nova Scotia, but missa was not described until 1935 from a series taken in Massachusetts. The names pallida (Banks) and coagulata (Prov.) are undoubtedly synonyms of difficilis. Considerable confusion arose at one time over the name

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coagulata as Hagen (in Lintner 1878) and Betten (1934) applied it to missa, but Provancher's description in 1877 was undoubtedly of difficilis, so the name was not available for this species.

The adult stage. Excellent descriptions with drawings of the two species are given by Schmid (1952) and Betten (1934), of difficilis by Betten and Mosely (1940), and of missa by Ross (1944).

The range of the genus seems to cover most of the north east. Adults of difficilis have been recorded from Nova Scotia, Maine, New Hampshire, Vermont, Massachusetts, Connecticut, New York, Pennsylvania, District of Columbia, and Virginia; missa is recorded from Maine, New Hampshire, Massachusetts, New York, Pennsylvania, Maryland, District of Columbia, Virginia, Illinois, Michigan, and Minnesota. It would seem that the only major difference in distribution is the westward extension of missa.

The larval stage. Lloyd (1921) has given a fairly complete description of the larva of difficilis, and Ross (1944) has described some of the salient points of missa. A more complete description of difficilis follows.

Length of mature larvae 14 mm., width 2.5 mm.; general shape eruciform; abdomen widest at the first segment, tapering slightly caudad; head and thoracic sclerites deep brown, legs pale brown, abdomen nearly white.

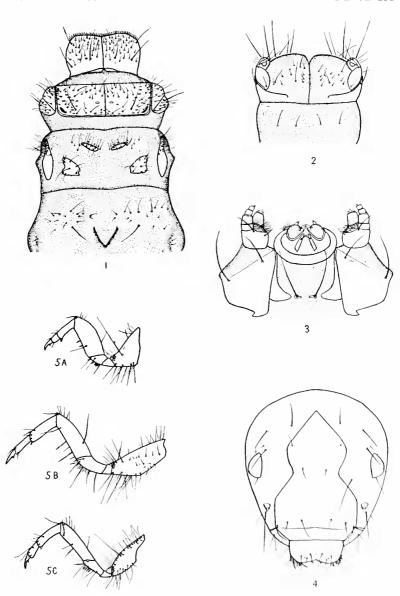
Head: broadly oval in frontal aspect; front rugose; with many very short, downward pointing setae; long dark setae arranged as in fig. 4. Many inconspicuous pale muscle insertion marks on posterior half; a circular group of 6–8 marks at apex of fronto-clypeus. Labrum light brown, rounded laterally; anterior margin emarginate medially. Six pairs of setae on dorsum: 3 on anterolateral margin, inner pair very short and broad; 2 in transverse row across center of labrum; one midway between marginal and central rows. Three pale spots or pits on dorsum; 1 median just anterior to transverse row of bristles; one caudad to each seta of the pair midway between the marginal and transverse rows. A brush of hairs on the margin mostly between the two posterior marginal setae. Mandibles heavy, dark brown, slightly asymmetrical. Two hairs near base of outer surface; brush of hairs on inner

Explanation of Plate IX

Fig. 1. Thorax and first abdominal segment, dorsal. Fig. 2. Anal prolegs, ventral. Fig. 3. Maxillae and labium, ventral. Fig. 4. Head, anterior. Fig. 5. Legs, posterior: A. fore leg, B. Middle leg, C. Hind Leg.

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PLATE IX



FRENESIA MISSA (MILNE)

surface of each mandible. Maxillae and labium with sclerotized parts light brown. Maxillary palpi 4-segmented (not 3 as shown in Lloyd (1921) fig. 109). Patch of fine hairs at base of maxillary lobe; its tip with numerous peg-like projections. Labial palpi 2-segmented.

Thorax: Pronotum with anterior margin shallowly emarginate; groove arising at point of articulation with leg and extending weakly over dorsum along posterior margin. Numerous short blade-like setae on notum, principally along anterior margin; a few longer setae scattered among them. Prosternal spine short, not extending beyond apices of front coxae. Mesonotum rectangular; low ridge extending around posterior margin and forward halfway on lateral margin; linear dark spot on postero-lateral angle. A few pale muscle attachment scars obliquely across middle; long dark setae scattered irregularly over surface. Metathorax with 3 pairs of small sclerites on dorsum; small ovate pair in anteromedial area, with 7–9 setae; larger roughly triangular pair posterior and laterad to first, with 8-9 setae; third pair on lateral margin, elongate, widened posteriorly, anteriorly with numerous setae. Legs paler than thorax; fuscus at articulation of femur and tibia, and coxa and trochanter. Fore legs shortest with femora considerably broadened; middle legs slightly longer than hind legs. Fore femora with 2 clear sword-like setae on ventral margin, these setae dark on other legs. All legs with brush of fine hairs on ventral apical portion of trochanters, a row of very short flattened setae along ventral margin of femora, and numerous long black setae on coxae and femora.

Abdomen: Fringe line present from third to eighth segments. Spacing humps of first segment small and flattened. Gills arranged as in fig. 10. First segment with a group of 6–10 setae on each side of dorsal hump; another group of 5 on upper surface of lateral hump; about 50 setae scattered over sternum. Mature larva with oval sclerotized rings on sternites 3–7. Posterior margin of eighth tergite with 20–25 setae. Ninth segment with 2–3 setae laterad of dorsal chitin plate.

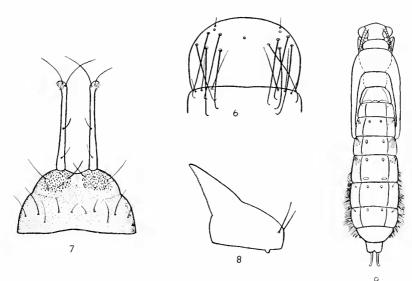
The larva of missa is very similar to that of difficilis differing in the following ways.

Explanation of Plate X

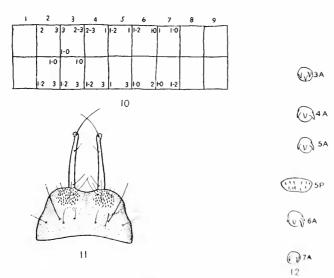
Fig. 6. Labrum, dorsal. Fig. 7. Caudal extremities, dorsal. Fig. 8. Mandible, dorsal. Fig. 9. Pupa, dorsal. Fig. 10. Larval tracheal gill diagram. Fig. 11. Caudal extremities, dorsal. Fig. 12. Hook plates, dorsal (A—anterior, P—posterior).

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PLATE X



FRENESIA DIFFICILIS (WALK.)



FRENESIA MISSA (MILNE)

Length of mature larva 11–12 mm., as opposed to 14–15 mm. Head (fig. 4) and mouthparts (fig. 3) morphologically identical, differing only in being smaller.

All thoracic sclerites (fig. 1) in general more hairy. At least 3 major setae laterad of anterior plates of metathorax. The long sword-like setae on posterior margin of femora clear yellowish on all legs (fig. 5).

First abdominal segment (fig. 1) more hairy; about 15 setae on each side of dorsal hump; venter with approximately 100 setae. Commonly with fewer gills but extremes exhibiting considerable overlap. An irregular row of 8–10 setae laterad of chitinous plate on dorsum of ninth segment. Each anal proleg with 10–12 setae on membranous ventral portion (fig. 2).

A possible relationship with *Glyphopsyche missouri* Ross, the only other described species in the *Chilostigma* group of genera, is suggested by the common character of short blade-like setae on the prothorax. The character of the setae on the ventral portion of the anal prolegs, used by Ross (1944) for separation of the genus *Frenesia*, is a specific character of *missa* only. Ross' key may be corrected by substituting the following for couplets 5 and 6.

The pupal stage. The pupa of difficilis has been superficially described by Lloyd (1921); that of missa, not at all. The following is a description of difficilis.

Length 13–15 mm., width 2–2.5 mm. Color creamy white, turning golden brown near time of ecdysis.

Head: Labrum (fig. 6) semicircular. Each distal bristle group of 5 long, stout, hooked setae; each proximal group of 3 slender setae. A very short seta on each side of labrum anterior to distal bristle group. Three pale spots: one posterior to each short seta, the third median. Mandible (fig. 8) inflated at base; apex thin, blade-like, with numerous serrations on the inner margin. A pair of black setae on outer surface near base. Front and vertex with 4 pairs of long black setae: first posterior to proximal bristle group of labrum; second antero-laterad of these; third between bases of antennae; last pair on vertex. Another pair of setae on epicranium near eyes; these may be accompanied by 1–2 short setae. Antennae extending posteriorly to caudal margin of seventh or eighth abdom-

inal segment; second antennal segment with tuft of 8-10 setae, longest seta about as long as segment.

Thorax: Pronotum with widely separated pair of setae. Mesoand metanotum each with a seta on each side near anterior margin; two setae on each side about midway to posterior margin. Coxae of fore legs with a group of 2-6 setae on lower surface; coxae of middle legs with 2 setae on ventral surface, one proximal, the other distal. A fringe of hairs on each side of tarsi of middle and hind legs. Wing pads extending caudally to anterior margin of fourth abdominal segment.

Abdomen: Segments 2-8 with 2 pairs of sclerotized rods: one pair dorsal, running from anterior to posterior margin of the segment (each rod overlies lateral margin of tergite of adult); second pair ventral, in a similar position. Strong lateral fringe beginning in posterior half of fifth segment, extending to caudal margin of eighth segment, curving ventrally there and ending near mid line. Gills present from anterior margin of second segment to anterior margin of seventh segment; arising either singly or in tufts of 2–3, about as long as segment which bears them. Hook plates present in anterior half of segments 3-7, number of hooks varying from 2-5, but usually 3 or 4; hook plate posteriorly on segment 5 with 8–11 hooks. Ninth segment with transverse row of 9–10 setae dorsally about mid-way of segment. Scabrous patch dorsally on ninth segment near base of anal processes with interspersed short hairs. Ninth sternum with 3 large, often flattened and twisted hairs near caudal margin. Anal processes (fig. 7) slender, rodlike, curved apically; almost 1½ times the length of ninth segment, cluster of short scabrous setae and two long hairs at apex; third hair near middle: a fourth in basal third.

The pupa of *missa* is the same as *difficilis* in structure, but shorter (12–13 mm.) and with shorter anal processes.

Anal processes (fig. 11) are subequal in length to the ninth segment. One long black seta at apex of each process. The two setae along the side of each process exhibit considerable variation in placement, often one or the other lacking.

Although many pupae have been described from this family, most descriptions are not sufficient to allow a separation of the genera. At present it is not possible to separate pupae of the genera Limnephilus, Glyphopsyche, and Frenesia.

Biology¹

¹ Unless otherwise stated the remarks apply equally well to both species.

The adult stage

Flight period. The time of emergence of the adults of this genus is very unusual, as no other caddis fly in the east flies so late in the year. Morse (personal correspondence) records the earliest date for difficilis, October 3, at Lee, New Hampshire. One of the paratype series at the MCZ in Harvard bears the earliest date found for missa, October 17, Ithaca, New York. In Sunderland, Mass. they become numerous in early November, declining in numbers late in the month. During December they are hard to find, though on warm days they may appear in numbers again. The latest date for difficilis is December 27, in Sunderland, Mass., and for missa it is February 2, in Michigan.

There are three known records of difficilis appearing in the spring: Morse & Blickle (1954), VI-24-46, Durham, N. H.; a specimen at the MCZ, VI-21, Glen Carlyn, Va.; and a specimen in the Univ. of Mass. collection, VI-23-54, Amherst, Mass. One record of a spring occurrence of missa is known: Leonard & Leonard (1949), VI-29, East Fish Lake, Mich. These individuals may represent small broods of these species which normally emerge in the spring, or, more likely, individuals that developed slowly and were prevented from emerging in the fall by cold weather.

The insects fly mainly during the daytime, but Morse & Blickle (1949) record taking several specimens of difficilis in a light trap. When not flying, they are found on grasses and herbs, which, being dead and brown in the fall of the year, render the protectively colored caddis flies very inconspicuous. When disturbed, the insects fall from their resting places and feign death, but if annoyed further they right themselves and attempt to escape by running or flying.

Temperature relations. Flight starts when the temperature rises to $45-55^{\circ}$ F. Only the males were taken at these temperatures, the females preferring temperatures about 10° higher.

The ability to withstand low temperatures is remarkable. Some individuals were left outdoors overnight in a bottle when the temperature dropped to about 20° F. In the morning they could hardly move, yet when taken indoors and warmed they were soon moving around normally. They may be found outdoors long after freezing has occurred, and in one instance an adult difficilis was seen walking over frozen ground.

Length of life. A series of experiments was performed in the laboratory to determine the length of life at room temperature (about 73° F.). Since no reared specimens of a known age were available, adults collected in the field were used. They were

placed in stender dishes with dried grass and a one-inch square of blotter moistened with water. Under these conditions 27 adults of *difficilis* lived an average of 7.5 days, one surviving 10 days. Seven adults of *missa* similarly confined lived an average of 6.1 days, one surviving 9 days.

Feeding. The specimens confined in the stender dishes were often seen to go through feeding motions on pieces of grass. An individual would move slowly across the grass, lapping or cleaning it with the haustellum in a manner similar to that of a fly. What they were obtaining, if anything, from the surface is not known.

In order to ascertain if supplementary nutrients would prolong their life, another series of experiments was performed using a sugar solution (33% sugar by volume) instead of water to moisten the blotter. With the sugar solution available 16 difficilis adults lived an average of 11.6, one surviving for 14 days. Five missa adults averaged 8.6 days, two surviving for 10 days. These results indicate an average increase of survival time of 4 days in difficilis and 2.5 days in missa, indicating they are able to utilize nutrients. Under natural conditions of low temperature and normal food, they may well live at least another several weeks.

Mating. Many times specimens were observed mating in a pint sized jar in which they were placed for transport to the laboratory. The process was never observed in nature but is doubtless the same as that described here.

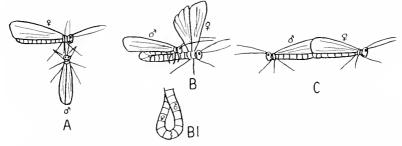
The male, when in proximity to the female, becomes very excited, running rapidly over the grass and bottle. Upon meeting the female he tries to grasp her with his front legs. If successful, he holds her at the bases of her front legs, usually from the right side, between the femora and tibia of his own front legs (fig. A). The body of the male is thus at about right angles to that of the female. The male possesses a row of spines on the inner surface of the femora and tibiae of the front legs. Apparently they allow him to grasp the female more securely. The head of the male is very close to the legs of the female, and sometimes he seems to be stroking the bases of her legs with his mouthparts. Next the female raises her wings and the male crawls onto the dorsum of her abdomen, facing the same direction as she (fig. B). At this point copulation takes place, the male's right side being attached to the female's left (fig. B1). The pair stays in this position for about one minute, whereupon the male crawls off on the side from which he mounted. They now assume the normal position, attached by their genitalia, and facing opposite directions (fig. C).

Often the male does not grasp the legs of the female as he should,

and she continues to move while he tries to correct his hold. Sometimes he succeeds, but often he does not and is dragged around for some time before he is brushed off. On some occasions the female fails to raise her wings and the male is shaken off despite all efforts.

It was noted several times that a male of one species would try to mate with the female of the other. In no instance were they able to copulate. Either the female would not raise her wings, or if she did and the male attempted to mate, they could not do so and soon separated. In one instance a male of *missa* was observed on the back of a male *difficilis* apparently trying to mate.

In the laboratory, duration of copulation may vary considerably, the pair generally remaining in copula for from one to one and one half days. A single case of extreme length of time was noted. A pair of *wissa* mated on November 6th and remained in copula until November 23rd, when the female was found dead and slightly



Figs. A–C. The mating positions of *Frenesia*. For explanation see text.

mouldy, still being dragged around by the male. In this case the pair must have been unable to separate, as it required considerable force to separate them.

One pair of difficilis was observed to mate twice. A mating pair was put into a container; a day later they separated. Four days afterward they were found in copula again and continued so for about 30 hours. No eggs were laid after either mating.

The egg stage

Oviposition. Oviposition was never observed, either in the field or in the laboratory. Only once was an egg mass laid in any culture. In this case a dozen adults of difficilis were confined in a screen cage 8-inches in diameter by 12-inches in height. A large clump of grass was placed on the bottom of the cage, and the whole cage placed in an aquarium with an inch of water on the bottom.

On the fifth day an egg mass was found on one side of the sod.

Appearance. The eggs are deposited in masses of 100–200, embedded in a gelatinous matrix. The masses when laid are about 2 mm. in diameter, spherical, yellow in color, with the eggs contiguous. As the gelatin absorbs water, the mass swells until it is about 20 mm. in diameter, remaining roughly spherical in shape, and varying in color from almost clear to light yellowish. The eggs are now separated by the gelatin by distances 2–3 times their diameters.

Habitat. The egg masses are deposited out of water, on soil or vegetation, as is typical for the family. A representative site was on grass roots and moss the overhung boards forming the sides of a pool. The eggs were three feet above water, and often occurred in groups of 4–6 masses in a small pocket, possibly where a pebble had fallen out. In other instances they were found partially covered by vegetation on dead grass and leaves an inch above water line. Large clumps of Juncus effusus L. growing in some of the pools were commonly used as oviposition sites. The masses were placed on the leaves about an inch above the water. The eggs were moist in all these situations, being either in seepage areas or on moist substrata.

Duration. Oviposition occurs during late November and December, but hatching is delayed until the following spring. The egg masses are often frozen solid during the winter, sometimes even having an ice cap. The exact time of hatching varies considerably depending on the season. It occurred in mid-March in 1954, but not until a month later in 1955. In 1955 the spice bush (Lindera Benzoin Blume) was coming into full bloom at the time of hatching, and it may well be a good indicator of when hatching will take place.

In order to determine how long the egg stage lasts under different conditions, egg masses were put into slender dishes with a little water to prevent desiccation. The dishes were then covered and kept at different temperatures. One series was kept at 23 °C., a second at 16.5°, and a third at 5°; these required 13, 22, and 35 days respectively to hatch.

The eggs do not undergo a true diapause during the winter. This fact was proven when a female difficilis laid an egg mass in the laboratory; this egg mass, which was never subjected to freezing temperatures, hatched in 22 days. It is thus cold and not a diapause which retards development and prevents hatching in the fall.

Hatching. The egg masses remain in a semi-solid state even if

submerged in water or alcohol for several months. They liquefy only when the emerging larvae start crawling through the mass. The eggs cease development and die if the mass is submerged in water for more than a day, and after a week the eggs are commonly surrounded by a halo of mold. Several masses that were hatching were placed in water. The larvae already hatched and the eggs containing larvae ready to hatch lived, but the rest of the eggs ceased development and soon died.

The larvae stay in or on the mass for a day or so after hatching. In no case were they observed to start building a case while in the jelly. The young larvae may be washed into the water by heavy dews or rains, as recorded by Wesenberg-Lund (1908) for the genus *Glyphotaclius*. However, some were seen crawling around in a dry petri dish several days after hatching. This observation suggests that the larvae may leave the egg mass and start searching for water,

The larval stage

Case-making. The first case made by the larva of difficilis consists of fine organic debris. The larva starts by scraping up a mass of debris with its legs. The mass is then cemented by the larva rolling it around with its front legs and mouthparts, spinning silk over it. When the condition of the mass is suitable the larva curls into a "C" shape, and by spinning silk over the debris attaches the mass around the middle of its abdomen. The larva is still uncovered at both ends, but more debris is attached to the first band, eventually completing the case. If another larva happens by, the first is not averse to collecting some material from the newcomer's case for its own. The process of casemaking is rapid, the first case being completed in about 15 minutes.

Within several days, larger pieces of plant material are added to the case increasing its rigidity. These pieces of plant material are attached at irregular angles, so that a case has a rather ragged appearance. These smallest cases consist almost completely of organic material: pieces of wood, leaves, seeds, and bark; one larva had even added a beetle elytron to form one side of the case. By the end of the first stadium sand grains are being added, and at maturity the case is in a large part mineral matter, with pieces of plant material here and there.

The larva of *missa* constructs its case from sand grains normally, not plant material, and may continue to do so throughout its life. For this reason the two species can often be told apart by the type of case. However, on certain occasions *missa* will make a case

like that of *difficilis*. At maturity the cases can often be separated as the larvae of *missa* utilize a preponderance of small equidimensional sand grains, while those of *difficilis* use larger, often flattened pieces of rock in its cases.

Habitat. Available records indicate that larvae develop in clean unpolluted water only. Lloyd (1921) reported difficilis in a small stream flowing out of a sphagnum bog. Ross (1944) records missa as occurring in a seepage area as well as in a stream nearby. Both species occur at the fish hatchery in streams and pools that are spring-fed and unpolluted.

The larvae of *missa* seem to prefer the streams and seepage areas. Ross (1944) states ". . . the larvae were congregated in a little seepage area near the bank and were thriving in water scarcely deep enough to cover their cases. Many individuals were feeding on leaves and twigs so that most of the insect and its case was actually out of water. Later we found that odd specimens would live in the stream itself; and, since the seepage areas frequently dried up, it is possible that the reservoir in the stream is chiefly responsible for the preservation of the species in this area." At the fish hatchery, the larvae of *missa* were not observed in large enough numbers in the streams to sustain the adult populations found in the same area. Even though it is likely that larvae develop in some of the many seepage areas present at the fish hatchery, no specimens were found in such locations by this investigator.

The records for *difficilis* indicate that the larvae always occur under water and not in seepage areas. Lloyd (1921) recorded larvae in certain portions of a small brook only. They were numerous in certain pools and in most of the brooks at the fish hatchery.

Food. The food of the larvae seems to be mostly dead organic matter. Ross (1944) records *missa* as feeding on leaves and twigs. On the basis of stomach examinations Lloyd (1921) stated that difficilis fed on leaves and decaying wood. All observations and dissections of specimens from the fish hatchery by the author corroborated these statements.

Duration. The larvae are first found in the spring from mid-March through April; the exact date depends on the season. Development proceeds rapidly during the summer, and the larvae mature in September and October. Based on measurements of head capsules, five larval instars are recognizable. The species are not separable until the third instar when the setae develop on the prolegs.

The pupal stage

Pupation. When ready for pupation, the larva attaches the an-

terior end of its case by silken threads to a rock, root, stick, or other vegetation. The ends of the case are then closed with sand grains, and a silken web woven over the inside. Ten or a dozen small openings are left at each end between the grains; these allow the water to circulate through the case.

Habitat. The larvae of difficilis which developed in a small pool seemed to favor the submerged bases of clumps of Juncus effusus L. for pupation. Dozens of pupae may be found attached at all angles to the leaves and roots at the base of such a plant. Often the larvae burrow beneath small stones and the resulting pupae may be found attached under such stones.

The larvae which develop in streams commonly attach to stones; however, one mass of roots, covered by their cases, was discovered in one of the brooks. Lloyd (1921) described a very similar instance.

The pupae of *missa* are found in conjunction with those of *difficilis* in the streams. They were also observed attached to corners and crevices in the boards along the sides of some pools where they might be three feet above water. In some cases water was trickling over them, but in others they were simply on very moist substrata.

Duration. Pupation does not occur immediately after attachment of the case by the larva. A brief prepupal stage of 1–2 weeks intervenes; the prepupae may be found in late September or early October.

The pupal stage itself lasts 3–4 weeks; pupae may be found in October and November.

Emergence. The pupa leaves its case by cutting away the anterior end, though at times it may emerge laterally. A few strands of silk are often left holding the end so that a "door" swings back into place after the pupa has left. It then swims to some emergent object where it crawls out of the water a distance varying from a quarter of an inch to a foot or so. Next, it attaches itself to some irregularity in the substratum by its front tarsal claws. When the time for ecdysis comes, which may be either immediately or 15–20 minutes later, pumping motions begin in the abdomen and sweep forward. The whole body moves forward slowly until the front legs hold the body from further forward movement. integument splits along the mid-dorsal line of the thorax, and the adult emerges rapidly. The front legs are the first to emerge, followed rapidly by the antennae and middle legs; the hind legs, wings, and abdomen are freed last. The wings as they emerge from the pupal skin are fully expanded, although not yet fully colored and hardened. The process of ecdysis takes only 4-5 minutes if nothing -----

unusual happens; however, the pupa may fall back into the water if it is not attached securely.

When large numbers of individuals are emerging, the exuvia may form a line on an object suitable for emergence. On the boards forming the dam of a pool where difficilis bred such a line was evident just above and parallel to, the water's edge, while other exuvia were scattered intermittently farther up.

SUMMARY

Descriptions with illustrations are given of the larvae and pupae of the two species of *Frenesia*. The winter period of the life cycle is passed in the egg stage, the larvae hatching in April or March and pupating in September or October. The adults are on the wing in late October through December, and rarely into January or February. Other aspects of the biology of the adult, egg, larval, and pupal stages are presented.

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ANNOUNCEMENT

The Council of Biological and Medical Abstracts Ltd. has decided to change the title of their journal British Abstracts of Medical Sciences to

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